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RECONSTRUCTING PALEODIET IN GROUND SLOTHS (MAMMALIA, XENARTHRA) USING DENTAL MICROWEAR ANALYSIS

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ABSTRACT

Understanding the paleoecology of extinct xenarthrans, such as ground sloths, is complicated because they lack living analogues. Previous studies have applied functional morphology and biomechanical analyses to reconstruct the diet and lifestyle of ground sloths, yet the application of dental microwear as a proxy for feeding ecology in extinct xenarthrans remains understudied. Here, we hypothesize that dental microwear patterns are statistically different among extinct ground sloths, thereby providing new evidence of feeding ecology in these animals. In a blind study, the dental microwear patterns in three extinct taxa representing two clades [*Megalonyx wheatleyi* and *Acratocnus odoutrigonus* in Megalonychidae, *Thinobadistes seguis* in Mylodontidae] were quantitatively analyzed using scanning electron microscopy at 500× magnification. Two independent observers recovered similar relative trends in microwear patterns between *M. wheatleyi*, *A. odoutrigonus*, and *T. seguis*, with mean number of scratches and feature width being the most informative variables among taxa. Microwear patterns in *M. wheatleyi* correspond most closely with living selective xenarthran herbivores (i.e., *Bradypus*), with a low number of scratches but a high feature width. *T. seguis*, in contrast, has an unusually high number of scratches but low feature width, which is unlike any patterns exhibited by living xenarthrans and indicates possible grazing habits. *A. odoutrigonus* falls between these two extremes, which we interpret as a more generalized browser, similar to *Choloepus*. Microwear patterns among living and extinct sloths sampled to date seem to fall along a continuum of herbivorous feeding strategies, with grazing and selective browsing representing the two extremes. Although we only examine three taxa, our results (stemming from a blind analysis that accounts for observer error) support the feasibility of using high-magnification dental microwear to examine feeding ecology in extinct ground sloths.

Introduction

Xenarthrans form a major clade of placental mammals (Delsuc et al., 2002) that include extant armadillos, tree sloths, and anteaters, as well as the extinct ground sloths, pampatheres, and glyptodonts (McKenna and Bell, 1997). Among other specialized traits, such as xenarthrous articulations of the spinal column and the articulation between the transverse processes of the proximal caudal vertebrae with the ischium (Vizcaíno and Loughry, 2008), xenarthrans are differentiated from other mammals by the absence of enamel on their adult teeth (Hillson, 2005). Although several clades of placental mammals have evolved partial or

complete enamel loss on their teeth (Hillson, 2005; Green, 2009a; Ungar, 2010), xenarthrans are unique in the almost universal enamel loss within the clade (Vizcaíno, 2009). The orthodontine that composes the surface of xenarthran dentition is a softer tissue than enamel (Hillson, 2005; Kalthoff, 2011), which causes their teeth to wear much faster compared to the enamel-covered teeth of other mammals. This wear is compensated for by the presence of an open root, which allows for continuous growth of the tooth throughout the life of the animal. Because dentition functions mainly to process food, the unique, soft, simple-shaped morphology of xenarthran teeth begs the question as to what food items

extinct members of this group consumed. Although ground sloth taxa are numerous in the Cenozoic fossil record in North and South America (McDonald and De Iuliis, 2008), understanding the paleoecology of these extinct mammals is complicated because they lack exact living ecological analogues.

Ground sloths inhabited a wide range of environments, stretching from Alaska to Argentina (McDonald and De Iuliis, 2008), including the Caribbean islands (White, 1993) and possibly Antarctica (Vizcaino and Scillato-Yane, 1995; MacPhee and Regeuro, 2010). Hypothesized eating habits ranged from grazing (Webb, 1989; Shockey and Anaya, 2011) and forest browsing (McDonald, 1995; Hoganson and McDonald, 2007) to aquatic feeding (Muizon et al., 2004), and ground sloths could have reached large sizes (approximately 1000–6000 kg in some taxa; Fariña et al., 1998). Their closest living relatives, the extant tree sloths, however, are limited to arboreal habitats in tropical climates (Vizcaino et al., 2008) and are relatively small compared to ground sloths (Gaudin and McDonald, 2008). Previous studies have applied functional morphology and biomechanical analyses to reconstruct life history in ground sloths (Naples, 1989; Vizcaino et al., 2006; Bargo et al., 2006a, b; Shockey and Anaya, 2011). As noted by Smith and Redford (1990), anatomy may not always be an accurate predictor of feeding ecology in extant xenarthrans. Therefore, it is important to pursue as many independent lines of evidence when examining diet in extinct xenarthrans.

One recent, new line of analysis that is being used to help better understand paleodiet in xenarthrans is dental microwear. Dental microwear refers to the microscopic scarring of the occlusal surface of teeth due to tooth-on-food or tooth-on-tooth interactions during mastication and can take the form of scars, such as scratches and pits of various widths, lengths, and orientations (Teaford, 1991). The type and density of microwear features depends on several factors, including, but certainly not limited to, the amount of oral processing and the frequency of abrasives in the diet. The longer an animal chews its food (i.e., oral processing), the more microwear features should be deposited on the chewing surface of the tooth (Teaford, 1991). The toughness of food particles also directly affects microwear, as tougher, more abrasive foods (e.g., grasses) are correlated with higher levels of tooth scarring (Ungar et al., 2008). For this reason, browsers (herbivores that consume tender leaves, fruits, etc.) should exhibit a lower density of microwear features than grazers (herbivores that primarily eat tough, abrasive grasses), as the grazer will use more oral processing to break down tougher foods (Solounias et al., 1988; Teaford, 1991; Ungar, 2010). Ingested grit from other sources including digging for food (such as roots or insects) or dust on low-level vegetation is also a major contributor to microwear formation (Williams and Kay, 2001). It is also possible that the acidity of fruits in an animal's diet will partially erase microwear (i.e., acid etching; Teaford, 1988). Analysis of microwear patterns can be done either qualitatively (describing overall texture or complexity), or quantitatively by measuring the size and density of features (Teaford, 1991). When applied to living organisms, it is possible to correlate specific diets with unique microwear patterns; this data can be used as a foundation for reconstructing the paleodiet of extinct taxa (e.g., Solounias et al., 1988; Solounias and Semprebon, 2002; Green et al., 2005).

While dental microwear is a well-established proxy for feeding patterns in mammals with enamel-covered teeth, the significance of microwear on softer orthodontine has received comparably less

attention, until recently (Oliveira, 2001; Green, 2009b, 2009c; Green and Resar, 2012). Initial microwear studies on xenarthrans (Oliveira, 2001; Green, 2009b; Green and Resar, 2012) show that these enigmatic mammals do record scars on their teeth that are similar in size and appearance to those observed in other mammals with enamel. Further, orthodontine microwear patterns in these animals can be statistically differentiated between taxa with different diets, although the resolution is not as high as that found in enamel studies that apply the same methodology (Green, 2009b; Green and Resar, 2012). These initial findings support the use of dental microwear as a proxy for xenarthran paleoecology. Most recently, Green and Resar (2012) examined microwear patterns in five extant species, each grouped into one of four dietary categories. Folivores consisted of *Bradypus variegatus* (Linnaeus, 1758), which consumes leaves from a narrow range of plant species (Chiarello, 2008). Frugivore-folivores were represented by *Choloepus didactylus* (Linnaeus, 1758) and *C. hoffmanni* (Peters, 1858), which eat a more variable mixture of fruits, leaves, and flowers (Chiarello, 2008). Among armadillos, insectivores were represented by *Dasylops novemcinctus* (Linnaeus, 1758), which primarily consumes insects, although some opportunistic omnivory does occur in this group (McDonough and Loughry, 2008). Carnivore-omnivores were represented by the armadillo *Euphractus sexcinctus* (Linnaeus, 1758), which has a more variable omnivorous diet relative to other cingulates (McDonough and Loughry, 2008). The authors concluded that relative differences in the number of scratches and width of scar features was useful in statistically differentiating not only xenarthrans living in distinct habitats (i.e., semi-fossorial armadillos versus arboreal tree sloths), but also taxa living in the same habitat (e.g., two-toed tree sloths versus three-toed tree sloths; Green and Resar, 2012). On average, insectivorous armadillos had a lower scratch count and higher feature width than armadillos classified as carnivore-omnivores. Likewise, folivorous three-toed sloths consistently had lower scratch density with a greater feature width than frugivore-folivorous two-toed sloths (Green and Resar, 2012).

Using data from Green and Resar (2012) as a foundation, we hypothesize that dental microwear patterns can be differentiated among extinct ground sloths, thereby providing new evidence of feeding ecology in this group. We test this hypothesis by quantifying and statistically comparing microwear patterns in three extinct ground sloth species with microwear in living tree sloths (with the latter taken from Green and Resar, 2012), using the same methodological approach as Green and Resar (2012). Originally, we sampled six extinct taxa for this study (see Appendix). However, post-taphonomic screening sample sizes for three of the taxa (*Hapalops*, *Octodontotherium*, and *Scelidotherium*) were insufficient to provide objective information about paleodiet, yet the data from these few specimens can still help identify methodological error in our analysis. Microwear patterns in the remaining three taxa (*Acratocnus*, *Megalonyx*, and *Thinobadistes*) were analyzed in detail, and we use data from these three species to test our hypothesis. We directly compared ground sloth microwear with data from Green and Resar (2012) for extant xenarthrans to accomplish this goal. The hypothesized paleoecology for the three primary study taxa is summarized below.

Megalonyx wheatleyi is a North American species of the clade Megalonychidae and includes several species with a wide geographic distribution from Mexico to the Yukon, including both east and west coasts (McDonald, 1995; Hoganson and

McDonald, 2007). Across its wide geographic distribution, *M. wheatleyi* has been reconstructed as a forest-dwelling browser (McDonald, 1995; Kohn et al. 2005; Hoganson and McDonald, 2007). *M. wheatleyi* specimens for this study come from the McLeod Limerock Mine in Levy County, Florida, which is middle Pleistocene (Irvingtonian) in age (Hulbert, 2001). As a hypothesized strict browser, we predict that *M. wheatleyi* should have a lower density of microwear features on its teeth relative to other ground sloths, an observation supported by data from living tree sloths (Green and Resar, 2012).

Acratocnus odontrigonus is also a member of Megalonychidae, and is considered more closely related to extant *Choloepus* (two-toed sloths) than to *M. wheatleyi* (Gaudin, 2004). While *Acratocnus* has a distribution across a number of the Great Antilles islands, this species is known only from the Quaternary of Puerto Rico (White and MacPhee, 2001). *A. odontrigonus* has been reconstructed as at least partially arboreal (White, 1993), but at this time, no hypotheses of paleodiet have been postulated for this species. *A. odontrigonus* specimens for this study came from Cerro Hueco Cave (Quaternary) in Puerto Rico (White and MacPhee, 2001), which, based on the associated fauna, represents an arid environment, characterized by savanna grasslands and dry scrub forests (Pregill and Olson, 1981). While the bulk of *Acratocnus* finds are from cave deposits, such a locality was probably not their typical habitat, as some sites implicitly indicate a trap environment (Anthony, 1916). Given the aboveground environments, semi-arboreal habits of these sloths, and morphological similarities to the feeding apparatuses of other megalonychids of all sizes (Bargo et al. 2006a, b; McAfee, 2011), we suggest *Acratocnus* was a folivorous browser.

Thinobadistes seguis is a mylodontid sloth from the Miocene of the Gulf Coastal Plain and southern Great Plains (Webb, 1989). During the Miocene, *T. seguis* occupied a complex mixed environment including forest, river, and open country (Webb et al., 1981). Very little has been published on *T. seguis*, but it has been hypothesized that mylodontids were grazers or bulk feeders in open habitats (Moore, 1978; McDonald and De Iuliis, 2008; Shockey and Anaya, 2011), although some species have been reconstructed as intermediate mixed feeders (Naples, 1989). More specifically, the broad, flat premaxilla and the correspondingly wide premental spout of the mandible that is indicative of Mylodontinae sloths, such as *Lestodou* and *Glossotherium* of South America, suggests a bulk grazing strategy (Bargo et al., 2006b). This muzzle morphology is also present in *T. seguis*, a species closely aligned with *Lestodon* (Webb, 1989; Gaudin, 2004). Specimens here come from Mixson's Bone Bed in Levy County, Florida, which is late Miocene (Hemophilia) in age (Hulbert, 2001; Morgan, 2005). Brief reports of the lithology of the Mixson's site appear to reflect a woodland savanna (typical of the late Miocene environments along the Gulf Coast; Webb 1977), yet detailed paleoenvironmental information about this location is currently lacking (Leidy and Lucas, 1896; R.C. Hulbert, Jr., personal communication).

Materials and Methods

Specimen selection

Twenty-three specimens from six taxa (*Megalonyx wheatleyi* [n=6]; *Acratocnus odontrigonus* [n=4]; *Thinobadistes seguis* [n=6]; *Octodontoherium grandee* [n=3]; *Hapalops elongates* [n=3]; *Scelidoherium* sp. [n=1]) were analyzed (Appendix 1). Specimens came from the vertebrate paleontology collections at the Field Museum of Natural History, Chicago, IL (FMNH) and the

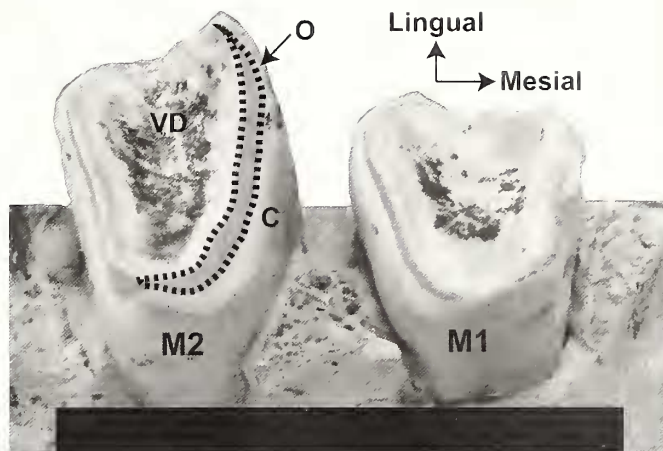


Figure 1. Representative image of upper sloth molariform (*Megalonyx*; UF 223806). Location of SEM imaging and analysis in this study was always along the orthodontine layer on the mesial facet of M2, indicated by the dashed crescent. Key: C, cementum; M1, molar 1; M2, molar 2; O, orthodontine; VD, vasodontine. Scale bar equals 3 cm.

American Museum of Natural History (AMNH), New York, NY. Following the approach standardized by Green and Resar (2012), we sampled only the mesial wear facet on upper second molariforms (M2; *sensu* Naples, 1982) for each taxon (Figure 1). For isolated teeth, we used direct comparison of *in situ* teeth in maxillae (available in the collections where sampling was conducted) to positively identify isolated M2s for our analysis, along with the following references: Anthony (1926); Hoffstetter (1956); McDonald (1977, 1987); Scott (1904); Webb (1989). All sample teeth for a particular species were chosen from the same locality, and while this did limit sample size, the authors felt that minimizing potential intraspecific variation in microwear patterns was necessary for this introductory study.

Specimen preparation

Cleaning, molding, and casting protocols for microwear analysis followed Green and Resar (2012). Resulting casts were mounted on 25.4 mm or 12.7 mm aluminum stubs, according to tooth size, using standard carbon adhesive tabs (Electron Microscopy Sciences, Inc). A belt of colloidal silver liquid (Electron Microscopy Sciences, Inc.) was applied to the base of the specimen and the top of the aluminum stub to improve electron dispersal and overall adhesion between the stub and the cast. The final preparation step, accomplished just before imaging, was to coat the specimen with a thin layer of gold (105 s) using a SEM Coating System (Microscience Division, Bio-Rad Laboratories, Inc.).

Scanning electron microscopy

For each tooth, two digital images along the outer orthodontine band (Figure 1) on the mesial wear facet on M2s were captured at 500 \times (with an operating voltage of 20 kV using secondary electrons) in an Amray Model 1600 Turbo scanning electron microscope located in McGilvery Hall at Kent State University. To standardize the counting area, a 100 μm \times 100 μm square was digitally constructed and centered over the area of highest density of visible microwear features in each image. This also allowed us

to select the most opportune location to sample ante-mortem microwear and to exclude areas with obvious casting artifacts. Brightness, contrast adjustments, and construction of the digital counting square were all accomplished using Adobe Photoshop CS4 and Adobe Illustrator CS4 (Adobe Systems, Inc.).

Controlling for taphonomic alteration

Since taphonomic processes can alter microwear patterns (Teaford, 1988), specimens were checked for possible false microwear by looking at non-occlusal surfaces of the tooth. Post-mortem abrasion is unlikely to affect only the chewing surface, so teeth that show similar microwear patterns on both the chewing and non-chewing surfaces were rejected due to the high likelihood of original microwear alteration (Teaford, 1988). In addition, if microwear was absent on the chewing surface of a tooth, the specimen was also considered altered and rejected, as ante-mortem microwear was most likely obliterated by taphonomic processes (King et al., 1999).

Microwear analysis

Following the methods of Green and Resar (2012), orthodontine microwear patterns on digital images were analyzed using the semi-automated custom software package Microware 4.02 (Ungar, 2002). This program was originally designed to quantify scratches and pits on enamel surfaces in mammals; however, the overall similarity of orthodontine microwear features to those in enamel (i.e., Oliveira, 2001; Green, 2009b, c; Green and Resar, 2012) supports the use of this program for this study. The Microware program involves a cursor-based user interface, where the researcher identifies endpoints of scratches and pits on the image. We focused on four variables recorded by the program: 1, number of scratches (S); 2, number of pits (P); 3, feature minor axis length, i.e., feature width (FW); and 4, degree of parallelism in feature orientation (R). Feature major axis length is automatically recorded by the program, but we did not analyze this variable because the endpoints of some scars extended beyond the 100 μm^2 counting square. We maintained a length/width ratio of 4:1 to discriminate scratches from pits.

Because the Microware program relies on human recognition of features, it is critical to account for operator error (Grine et al., 2002). Additionally, knowledge of specimen identification and dietary category assignment during analysis may lead to subconscious bias during data collection (e.g. Mihlbachler et al., 2012). As in Green and Resar (2012), we controlled for observer error in the following ways: 1) observers 1 (NAR) and 2 (JLG) independently counted microwear features on all images; 2) all images were randomly organized by an independent third-party (i.e., not an author) and the specimen number and species identity were removed prior to counting, thus creating a blind analysis. Ten randomly selected images were duplicated within the randomized image file. These duplicates were analyzed along with all other images, which allowed us to measure intraobserver error in the consistency of feature recognition by both researchers.

Eight non-parametric Wilcoxon signed-rank tests [one per variable (4) per observer (2)] were applied to determine if each observer consistently recognized the same numbers of features between iterations of the duplicate images. We did not re-analyze images more than once because repeated iterations can lead to observer familiarity with images, which can falsely deflate error measurements (Mihlbachler et al., 2012). Four Wilcoxon signed-rank tests (one per variable) were applied to test for significant

differences between observer datasets, providing a measure of interobserver error in absolute values of variables. We measured the degree of correlation between observer datasets by calculating one Pearson Correlation Coefficient (PCC) per variable; this reveals whether observers recovered the same differences between species studied, regardless of absolute values (e.g., Mihlbachler et al., 2012; Green and Resar, 2012). Following Grine et al. (2002), we also calculated the Mean Absolute Percent Difference (MAPD) per microwear variable between observers, which allows us to estimate whether some variables are more error-prone relative to others.

Both observers independently acquired data from the same images using a blind experimental design, so the discovery of similar microwear patterns means that the two observers consistently found the same type of data. This in turn suggests that additional individuals should be able to reproduce these results. Therefore, we analyze both observer datasets in the same statistical manner to provide the most error-free, objective conclusions possible using this analytical technique. Descriptive statistics were computed for both observer datasets for each variable in each dietary group. We used non-parametric Mann-Whitney U tests to determine if significant interspecific differences exist in each observer's dataset.

Finally, two canonical discriminant function analyses (DFA) were conducted (one per observer) to determine which microwear variables are statistically correlated with diet among extinct ground sloths. All four variables were included in the analysis, with taxon as the grouping variable. A Wilks' Lambda test was the metric of significance for resulting functions. All statistical tests in this study were conducted in a PC environment using SPSS (Statistical Package for Social Sciences, Inc.) version 19.0.

Results

Taphonomic alteration

Of the 23 specimens examined for this study, six (FMNH P13133, FMNH P13145, FMNH P13507, FMNH P13593, FMNHP 14450 (the only specimen of *Scelidotherium*), and AMNH 99186) showed post-mortem obliteration of original microwear, as described by King et al. (1999). One specimen of *M. wheatleyi* (AMNH 140855-C) had only one spot of observable microwear that was deemed genuine, so only one image was captured for this specimen, as opposed to two non-overlapping images for each of the remaining teeth. After taphonomic screening, *H. elongatus* and *O. grandae* were represented by only one specimen each in our sample. Ante-mortem microwear is visible on these two remaining specimens, so we included them (along with unaltered specimens from *A. odontrigonus*, *M. wheatleyi*, and *T. segnis*) in our analysis of intra- and interobserver error to provide the most comprehensive results. However, one tooth per species does not provide enough statistically useful information to reconstruct paleodiet, as there is no measure of populational variation in microwear. Thus, *H. elongatus* and *O. grandae* were not included in our statistical analysis of interspecific microwear patterns; only data from unaltered *A. odontrigonus*, *M. wheatleyi*, and *T. segnis* specimens were statistically analyzed for interspecific microwear differences.

Observer error

Wilcoxon signed-rank tests for intraobserver error revealed very little difference among variables between replicate images for either observer; only R varied significantly for observer 2

Table 1. Results from Wilcoxon signed-rank tests for significant differences in variables both between and among independent observers. Significant p-values are in bold. Variable abbreviations follow the text. Key: Z, z value.

Microwear variable	Observer 1		Observer 2	
	Z	p	Z	p
Intraobserver Differences				
FW	-0.26	0.80	-0.92	0.36
R	-0.46	0.65	-2.09	0.04
P	-1.72	0.09	-0.56	0.57
S	-0.26	0.80	-1.26	0.21
Interobserver Differences (Observer 1 vs. Observer 2)				
FW	-0.73	0.46		
R	-1.56	0.11		
P	-3.42	<0.01		
S	-3.01	<0.01		

(Table 1). However, two out of four variables (S, P) varied significantly between observers (Table 1). PCCs for each variable revealed a high degree of correlation between observer datasets though, with three of the variables (S, FW, R) being significant below the 0.01 level (Table 2). Mean P had the highest MAPD (42%; Table 3), while mean R had the lowest (3%; Table 3).

Microwear statistics

A total of 25 images from *M. wheatleyi*, *T. segnis*, and *A. odontrigonus* were analyzed for interspecific differences in microwear using descriptive, ANOVA/Welch and DFA statistical tests to address the hypothesis that there are significant differences between taxa that can be used to differentiate feeding ecology. For both observers, *T. segnis* had the highest scratch count and lowest feature width, whereas *M. wheatleyi* had the lowest number of scratches and greatest feature width (Table 4; Figures 2–3). For both of these variables, *A. odontrigonus* had intermediate values, relative to the other species (Table 4; Figures 2–3).

Mann–Whitney U tests revealed mean S and FW as statistically different between *M. wheatleyi* and *T. segnis* (Table 5). However, neither mean S nor mean FW could statistically distinguish *A. odontrigonus* from the other two analyzed taxa (Table 5). Observer 2 found that R and P were significant in distinguishing *A. odontrigonus* from *M. wheatleyi*, but observer 1 did not corroborate this result (Table 5).

To discriminate further between these three ground sloths, two canonical functions were formed by SPSS for each observer's DFA. Function 1 explains the majority of the variance and is statistically significant for both observers, whereas function 2 is never significant (Table 6). Mean S has the highest correlation with function 1 for both observers, with mean FW also correlated with function 1 only in observer 2 (Table 7). Both observers

Table 2. Pearson Correlation Coefficients (PCC) for data sets between Observers 1 and 2, organized by microwear variable. Significant p-values are in bold. Variable abbreviations follow the text.

Microwear variable	PCC	p
FW	0.76	<0.01
R	0.79	<0.01
P	0.40	0.11
S	0.77	<0.01

Table 3. Mean Absolute Percentage Differences (MAPD) for all variables between observers. Variable abbreviations follow the text.

Microwear variable	Observer 1	Observer 2	Combined mean	MAPD
S	20.76	30.35	14.78	18.76%
P	2.85	6.97	4.91	41.96%
FW	2.43	2.26	2.35	3.40%
R	0.72	0.68	0.70	2.85%

recorded a total percent correct classification of 93.30% for all specimens analyzed (Table 8).

Discussion

Observer error

With the exception of R for observer 2, both observers were able to consistently recognize and identify the same microwear variables on replicate images (Table 1). However, because R was not unanimously significant in diagnosing interspecific microwear in ground sloths (discussed further below; Table 5), significant observer variation in this variable does not hinder our overall analysis. Between observers, both mean S and P varied significantly (Table 1); such interobserver error is not uncommon, as similar error levels were present in the previous analysis of microwear in extant xenarthrans (Green and Resar, 2012) and have been also recorded in enamel microwear studies (e.g., Grine et al., 2002; Purnell et al., 2006; Muhlbachler et al., 2012). While S and P varied significantly between observers, it follows reason that FW and R would not vary as much. The expected average of a random sample from a population should be approximately the same as the mean of the entire population, regardless of sample size. Given that S and P are counts, they would differ significantly based on the number of features identified. However, FW and R, being averages calculated from a sample of features identified in the image, are approximate to the true mean for the entire image, even though the feature counts may differ between observers. FW and R should be similar between both observers because they are looking at the same image.

MAPD for our variables are relatively comparable with those reported in Green and Resar (2012), with the error being highest in P and S and lowest among FW and R (Table 3). However, absolute values for MAPDs in our study (with the exception of R) are higher than that of extant xenarthrans (Table 3). This increased relative error between observers may be inflated by the sheer density of microwear features in taxa such as *Thimobadistes* (Figure 3C), where number of fine-scale scratches is high, causing some inconsistency between observers.

However, even though interobserver variation is present, PCCs still revealed significant correlations for three variables (FW, S, R; Table 2). Thus, while absolute values may differ between observers, independent observers consistently identified similar relative patterns under blind conditions in our analysis. This finding, coupled with the presence of similar interobserver correlations in extant xenarthrans (Green and Resar, 2012), supports the application of high-magnification SEM microwear analysis for reconstructing paleoecology in ground sloths.

Variable significance

To avoid subjectivity in microwear studies, reproducibility in observer data should be assessed before interpretation and, ideally, only repeated results between multiple, independent observers should be accepted. Following these criteria, we can

Table 4. Mean values of microwear variables recorded by two independent observers for five extant xenarthran species (grouped by dietary category, labeled in bold in the specimen column). Variable abbreviations follow the text. Key: AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History.

Specimen	Observer 1				Observer 2			
	FW	R	P	S	FW	R	P	S
<i>A. odontrigonus</i>								
AMNH 17722	1.31	0.82	1.50	19.00	1.23	0.75	8.50	27.50
AMNH 94713	2.72	0.58	3.50	25.50	2.03	0.51	13.00	40.50
AMNH 17715	3.36	0.43	4.50	12.00	3.26	0.47	11.00	18.50
Group Average (SD)	2.46 (1.05)	0.61 (0.20)	3.17 (1.53)	18.83 (6.75)	2.17 (1.02)	0.58 (0.15)	10.83 (2.25)	28.83 (11.06)
<i>H. clongatus</i>								
FMNH P13122	1.56	0.84	2.00	46.00	2.17	0.57	4.00	30.00
<i>M. wheatleyi</i>								
AMNH 140854	3.01	0.95	1.50	14.00	2.10	0.79	5.50	23.00
AMNH 140855-A	3.18	0.84	2.00	8.50	1.92	0.72	2.00	16.00
AMNH 140855-B	3.29	0.81	6.00	9.00	3.63	0.93	7.00	10.50
AMNH 140855-C	2.97	0.85	0.50	11.50	2.13	0.76	5.00	36.00
AMNH 140855-D	2.40	0.97	1.50	14.00	3.02	0.96	7.00	16.00
AMNH 99186	5.24	0.60	4.50	5.00	3.70	0.93	7.00	11.00
Group Average (SD)	3.35 (0.98)	0.84 (0.13)	2.67 (2.11)	10.33 (3.52)	2.75 (0.81)	0.85 (0.10)	5.58 (1.96)	18.75 (9.58)
<i>O. grandae</i>								
FMNH P13583	2.42	0.64	2.50	11.00	2.86	0.40	7.50	15.00
<i>T. segnis</i>								
AMNH FAM 102658	1.69	0.60	4.00	28.50	1.45	0.64	10.00	57.00
AMNH FAM 102672	1.45	0.37	1.00	36.50	1.59	0.17	13.50	46.50
FMNH 28354	1.67	0.85	2.00	30.00	1.42	0.83	4.00	47.50
FMNH 34347	1.64	0.93	10.50	47.50	1.90	0.91	9.50	57.50
FMNH 34348	1.60	0.82	1.00	18.00	1.57	0.77	3.00	36.00
Group Average (SD)	1.67 (0.17)	0.65 (0.25)	3.08 (3.88)	29.58 (11.51)	1.73 (0.38)	0.62 (0.29)	6.83 (4.87)	45.33 (11.79)

be reasonably certain that our interpretations of paleodiet from microwear are as unbiased as possible (e.g., Mihbachler et al., 2012). In our study, although there is a high degree of correlation between observer datasets, there were some mixed results from statistical tests between observers.

Both observers found that variables S and FW revealed the same significant distinction among sampled ground sloths using Mann–Whitney U tests (Tables 5–8). In contrast, when DFA results are considered, the only variable that was shared between observers for function 1 (the only significant function in both analyses; Table 6) was FW. Variable S, in addition to FW, was important to function 1 only for observer 2 (Table 7).

We conclude that both variables FW and S have the highest significance in reconstructing paleoecology from microwear in extinct ground sloths. These two variables yielded significant results between observers, although the significance of each variable is, in some cases, dependent on the nature of the statistical test. Nevertheless, significant PCCs for S and FW suggest that both observers recorded the same relative patterns between species, which supports a genuine interspecific pattern. Although observer 2 found that R and P were significant between *A. odontrigonus* and *M. wheatleyi*, observer 1 did not corroborate this result (Table 5); this discrepancy, coupled with the presence of significant intraobserver error in R for observer 1 (Table 1) calls into question the validity of this result. Thus, R and P likely have no significance in distinguishing ground sloth taxa in our study and we do not consider these variables further in this study.

Interpretation of feeding ecology

Of the examined taxa, *Megalonyx wheatleyi* was most similar to extant xenarthran folivores (*Bradypus*) and frugivore-folivores

(*Choloepus*) through the presence of lower mean S and higher mean FW values relative to other sampled taxa (Table 5, Figure 2; Green and Resar, 2012). This result supports the hypothesis that *M. wheatleyi* was a forest browser. As a hypothesized browser, we predicted that *M. wheatleyi* should have less oral processing and hence a lower density of microwear features (Ungar et al. 2008). Since oral processing (or chewing) is correlated with the formation of microwear features, more chewing usually leads to more microwear features. Browsers, herbivores that are more selective about what plants they are eating and typically feed on softer leaves, have less need to chew and therefore are predicted to have fewer microwear features than grazers, who feed more indiscriminately and on tougher vegetation (Teaford, 1991; Ungar et al., 2008). We support this prediction, reporting lower feature density in *M. wheatleyi*, relative to other ground sloths (Figure 3), which results from a significantly lower number of scratches (Tables 4–6). Consuming a large quantity of tough branches or twigs may account for relatively wider scars in *M. wheatleyi* relative to *A. odontrigonus* and *T. segnis*. The similarity of *M. wheatleyi* to both extant sloths suggests that it may have had a more varied diet than *Bradypus*, but less varied than that of *Choloepus*. In contrast to extant sloths, however, *Megalonyx* would have been feeding at a much lower level (i.e., ground-dwelling niche; Hoganson and McDonald, 2007), so a larger and/or different selection of available browse may be reflected by microwear. Overall, our results support previous hypotheses, drawn from independent lines of evidence (e.g., Hoganson and McDonald, 2007), that *M. wheatleyi* occupied a forest browsing niche during the Quaternary in Florida and likely in other parts of its North American distribution (e.g., Kohn et al., 2005).

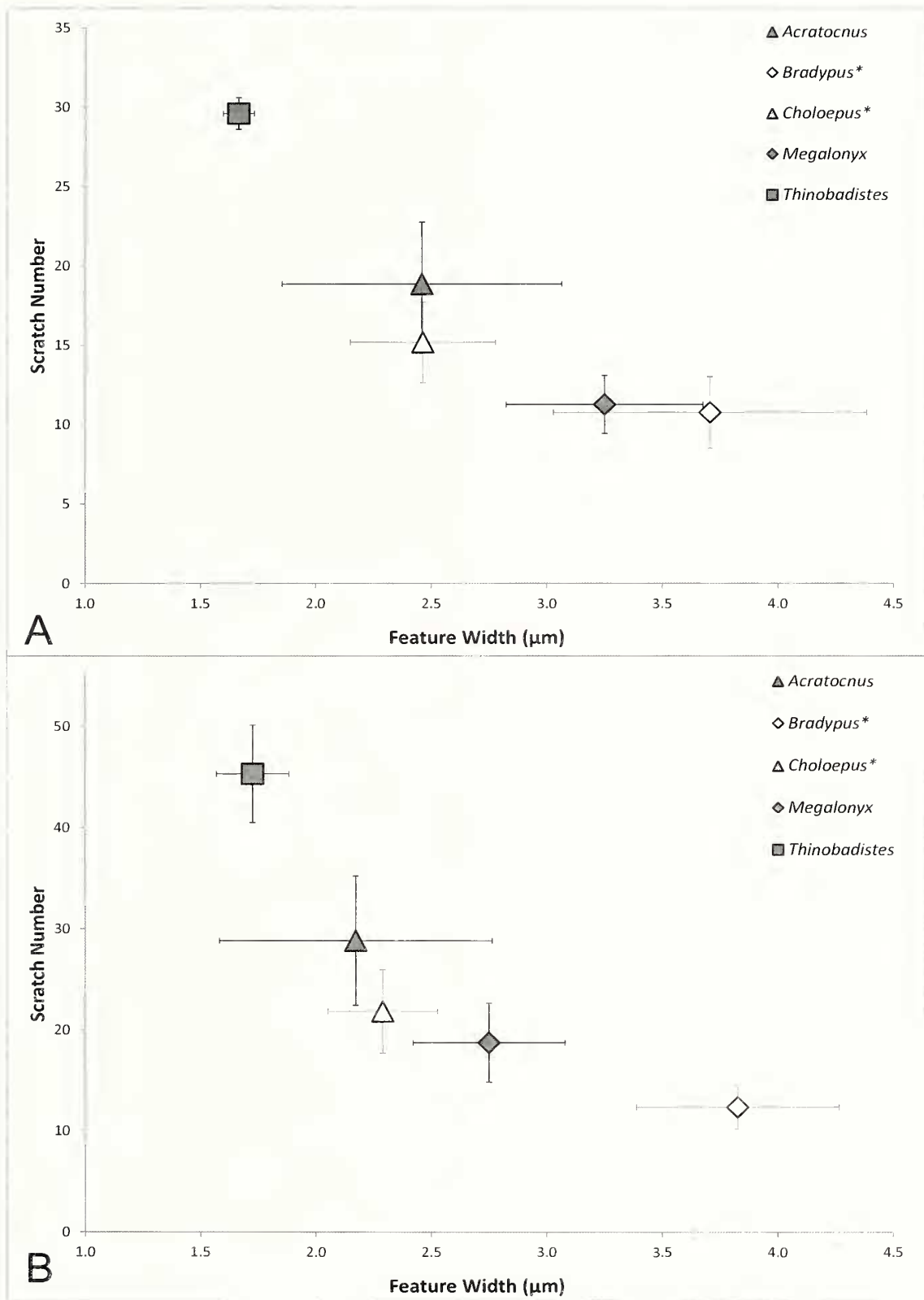


Figure 2. Graph of mean feature width (FW) vs. scratch number (S) for both observers; A, Observer 1; B, Observer 2. * denotes extant taxa (taken from Green and Resar, 2012).

Microwear in *Thinobadistes segnis* was anomalous in that we consistently observed thinner scratches in a much higher density on its teeth than any other sampled xenarthran to date, both extinct and extant (Table 4; Figures 2–3). Mylodontids are

considered general grazers (Moore, 1978; McDonald and De Iuliis, 2008; Shockey and Anaya, 2011) or possibly mixed feeders (Naples, 1989), diets usually correlated with increased oral processing relative to browsers (Ungar et al., 2008). A relatively

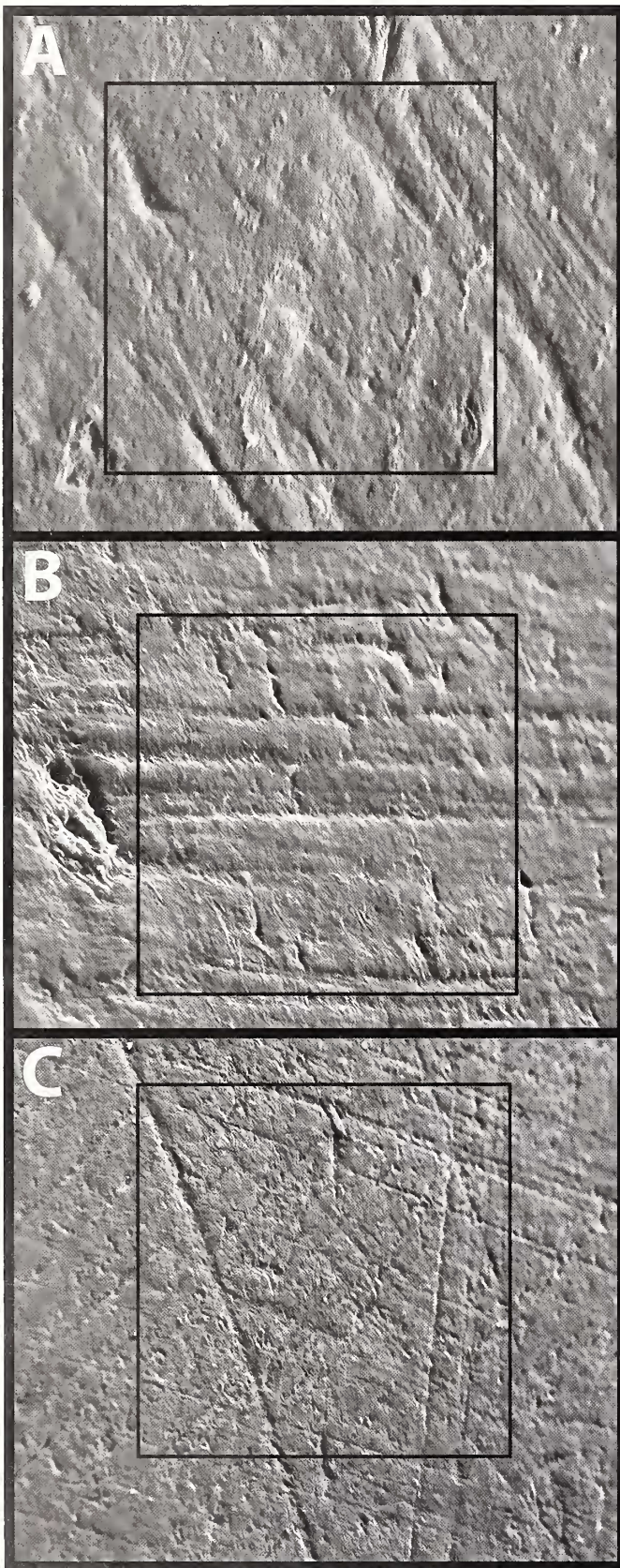


Figure 3. Examples of dental microwear on ground sloths M2s taken at 500 \times ; black square represents the 100 μm \times 100 μm counting square; A, *Megalonyx wheatleyi* (AMNH 140855-A);

Table 5. Mann–Whitney U tests for data from both observers. Significant p-values are in bold. Variable abbreviations follow the text. Key: Z, z value.

	Observer 1		Observer 2	
	Z	p	Z	p
<i>Acratocnus</i> vs. <i>Megalonyx</i>				
S	-1.82	0.07	-1.56	0.12
P	-0.40	0.70	-2.36	0.02
FW	-0.78	0.44	-1.03	0.30
R	-1.81	0.07	-2.07	0.04
<i>Acratocnus</i> vs. <i>Thinobadistes</i>				
S	-1.29	0.20	-1.69	0.09
P	-0.78	0.44	-1.03	0.30
FW	-0.78	0.44	-0.52	0.61
R	-0.39	0.70	-0.52	0.61
<i>Megalonyx</i> vs. <i>Thinobadistes</i>				
S	-2.89	<0.01	-2.65	0.01
P	-0.40	0.69	-0.32	0.75
FW	-2.88	<0.01	-2.40	0.02
R	-1.29	0.20	-1.60	0.11

high scratch density in *T. segnis* supports high amounts of oral processing (Ungar et al., 2008), which in turn suggests the possible inclusion of tough, abrasive vegetation, such as grass, in the regular diet of this taxon (Solounias et al. 1988). Therefore, it is possible that *T. segnis* occupied a mainly grazing niche in the Miocene savannas of Florida. However, we note that the correlation between high scratch density and grazing only exists in enamel-based microwear studies (Solounias et al., 1988; Teaford, 1991; Solounias and Semprebon, 2002); there are no extant grazers that have teeth composed solely of orthodentine, so it is difficult to fully test this hypothesis. As an alternate hypothesis, the high scratch density and relatively low FW could come from the consumption of high amounts of fine-scale grit, which accumulates near ground level in open habitats (Williams and Kay, 2001). The paleoenvironment of Mixson's bone bed is not as well understood as that of contemporary Miocene environments in Florida (e.g., Love Bone Bed; Hulbert, 2001), yet current evidence suggests an open, savanna-like environment (Leidy and Lucas, 1896; R.C. Hulbert, Jr., personal communication). This observation, coupled with smaller body size (about 450 kg; McDonald, 2005) that suggests low-level feeding habits (e.g., Webb, 1989), supports the inclusion of grit during feeding, and/or possibly a diet that consisted mainly of abrasive grasses and vegetation. *T. segnis* may very well have been a grazer in the Miocene grasslands, but supporting empirical evidence for grazing in this taxon is currently lacking.

Acratocnus odontrigonus most closely resembled extant frugivore-folivores (*Choloepus*) in terms of S and FW (Figure 2). The predicted lifestyle of *A. odontrigonus* is at least semi-arboreal, and may have been somewhat similar to the obligate arboreal role of living two-toed sloths (White, 1993). Among extant xenarthrans, microwear patterns are significantly different between ground-dwelling forms versus strictly arboreal taxa, thereby reflecting habitat occupancy as much as dietary differences (Green and Resar,

←

B, *Acratocnus odontrigonus* (AMNH 17715); C, *Thinobadistes segnis* (AMNH FAM 102672).

Table 6. Variance and significance of generated discriminant functions for each observer's DFA. Significant p-values are in bold. Key: %V, percent of total variance described by each function; df, degrees of freedom; p, p-value; WL, Wilks' Lambda value.

Function	Observer 1				Observer 2			
	%V	WL	df	p	%V	WL	df	p
1	97.30	0.14	8	<0.01	80.30	0.14	8	<0.01
2	2.70	0.88	3	0.71	19.70	0.58	3	0.12

2012). Our results support the view of *A. odontrigonus* occupying at least a semi-arboreal habitat in the Quaternary of Puerto Rico. However, we exercise caution in assuming that *Choloepus* and *A. odontrigonus* had similar diets, because the West Indies during the Quaternary were much drier than the tropical regions where *Choloepus* resides today (Pregill and Olson 1981). It is possible that *A. odontrigonus* was herbivorous and engaged in a browsing folivorous habit akin to that of *Choloepus* due to their close phylogenetic affinity (White et al., 2001; Gaudin, 2004), and the differences perhaps reflect different amounts of grit or abrasive particles within the opposing plant matter constituting the two diets. *Neocnus*, another Caribbean megalonychid with close affinities to *Acratocnus* and *Choloepus* (White and MacPhee, 2001; Gaudin, 2004), has also been suggested as an arboreal folivore but with a feeding strategy more similar to that of *Bradypus* (McAfee, 2011), further highlighting the potential differences for dietary strategies and the need for independent lines of evidence.

Of the three taxa statistically analyzed (*M. wheatleyi*, *T. segnis*, and *A. odontrigonus*), only *M. wheatleyi* and *T. segnis* were statistically differentiable (in terms of S and FW; Table 5). This leaves *A. odontrigonus* as indistinguishable from the other two taxa (Table 5). There are two probable explanations for this occurrence. First, *A. odontrigonus* has values for S and FW in between *T. segnis* and *M. wheatleyi* (Figure 2) and thus has less of an absolute difference between its mean values and those of *T. segnis* and *M. wheatleyi*. Second, *A. odontrigonus* was represented by fewer specimens than either *T. segnis* or *M. wheatleyi* in our study (Table 4), which may obscure statistical significance.

In addition, S vs. FW plots between observers reveal a repeated trend, in that microwear patterns among xenarthrans (both living and extinct) appears to exist on a continuum (Figure 2). *Bradypus* represents one extreme of this spectrum, whereas *T. segnis* represents the other extreme, with *Acratocnus*, *Choloepus*, and *Megalonyx* occupying the middle range (Figure 2). The diet of living *Bradypus* and *Choloepus* is selectively folivorous in the former and more generalized browsing in the latter. It is possible

Table 7. Discriminant function structure matrix. Values marked with an asterisk (*) reveal the largest absolute correlation between that variable and the corresponding discriminant function. Variable abbreviations follow the text.

Function	Observer 1		Observer 2	
	1	2	1	2
FW	0.47*	-0.40	0.70*	-0.32
S	-0.50	0.66*	-0.38*	0.32
R	0.22	0.59*	-0.14	-0.72*
P	-0.34	-0.86*	-0.24	0.59*

Table 8. Probabilities from DFA classification matrix for each observer. Bold values indicate total percent correct classification per taxon.

Observer	Taxon	<i>A. odontrigonus</i>	<i>M. wheatleyi</i>	<i>T. segnis</i>
1	% Correct			
	<i>A. odontrigonus</i>	100.00	0.00	0.00
	<i>M. wheatleyi</i>	0.00	100.00	0.00
	<i>T. segnis</i>	16.70	0.00	83.30
2	% Correct			
	<i>A. odontrigonus</i>	100.00	0.00	0.00
	<i>M. wheatleyi</i>	0.00	83.30	16.70
	<i>T. segnis</i>	0.00	0.00	100.00

these graphs represent a browser-grazer continuum of herbivorous feeding strategies in xenarthrans, with selective browsers (*Bradypus*) representing the lower right extreme and grazers occupying the upper left extreme. In this scenario, *T. segnis* would be a grazer, whereas *Choloepus* and *Acratocnus* (existing near the middle of the continuum) might be interpreted as more generalist browsers. *Megalonyx* always occupies the space between *Choloepus* and *Bradypus*, suggesting (under this scenario) that it was a more specialized browser than *Choloepus*, but less so than *Bradypus*. This last interpretation mirrors paleoecological reconstructions of *Megalonyx* from independent lines of evidence (e.g., Kohn et al., 2005; Hoganson and McDonald, 2007). It is also interesting to note that Figure 2 also separates the sloths into phylogenetic groupings with the megalonychids (*Acratocnus*, *Choloepus*, and *Megalonyx*) all occupying the middle range while the extremes are held by a mylodontid (*Thinobadistes*) and a bradypodid (*Bradypus*), which could indicate that portions of the feeding spectrum have their roots in phylogenetic relationships. These hypotheses remain to be tested by future microwear studies and increased analysis of paleodiet in sloths by applying this technique to a wider variety of taxa.

Conclusions

To our knowledge, this is the first time that microwear patterns of multiple extinct ground sloths have been analyzed and statistically compared to data from living xenarthrans to better understand the paleoecology of this group. Our results support high-magnification orthodontine microwear analysis as a valid method of examining diet in xenarthrans, given a large enough sample size. The previously hypothesized lifestyle of *M. wheatleyi* as a forest browser (McDonald 1995; Hoganson and McDonald, 2007) is supported by a low number of scratches and wide scars, a pattern that is quantitatively identical to microwear in living folivorous three-toed sloths. Additionally, we suggest that a high number of scratches and lower scar width in *T. segnis* suggests high levels of grit in the diet, either from dust accumulating on ground level vegetation or from abrasive grasses, or possibly a mixture of these two suggestions. Our study focused on a limited number of available specimens from a narrow selection of taxa, which limits the overall conclusions that we can reasonably draw from our data. What is relevant at this time is that we must note that our respective ground sloths represent taxa from different ages, climates, and habitats (e.g., Pleistocene forests, tropical and temperate, versus Miocene savannas). Therefore, the drastic differences in microwear noted between *M. wheatleyi* and *T. segnis* may stem from intangible variation in environmental conditions, rather than strictly from diet. However, because orthodontine microwear reveals distinct feeding differences in living xenarthrans that occupy different environments (e.g., semi-fossorial armadillos versus arboreal

sloths; Green and Resar, 2012), we suggest that the differences we report here are reflective of differences in feeding ecology.

This initial work reveals that paleoecological signals should be recorded in fossil ground sloth teeth, provided post-mortem alteration has been taken into account. Future studies should look at a wider range of taxa that have more specimens available, including fossil cingulate taxa. We also suggest that future microwear studies in extinct xenarthrans examine different taxa that co-occur at the same locality, such as Rancho La Brea, rather than from chronologically different localities. Analysis of stable isotopes in xenarthran teeth may yield comparative information regarding paleodiet. Xenarthran orthodontine may be less prone to diagenetic alteration than originally assumed (MacFadden et al., 2010). However, there remain complications that need to be resolved before the geochemical signal of orthodontine can be objectively interpreted (MacFadden et al., 2010). More broadly, further investigation should be made into taxa that have been investigated with morphological methods, particularly the South American sloths (e.g., *Megatherium*, *Glossotherium*, *Myiodon*, *Hapalops*, and *Scelidotherium*), for which there is a large body of work (e.g., Bargo et al., 2006a, b; Vizcaíno et al., 2006). This would allow microwear analysis to be correlated against these already established methods, and would further our understanding of the usefulness of dental microwear as a tool for reconstructing feeding ecology in extinct xenarthrans.

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Appendix 1. Listing of all specimens sampled in this study, organized by species (with taxonomic authority). Institutional Abbreviations: AMNH = American Museum of Natural History, New York; FMNH = Field Museum of Natural History, Chicago.

Species	Specimen number	Locality
<i>Acratocnus odontrigonus</i> (Anthony, 1916)	AMNH 17715	Puerto Rico
	AMNH 17722	Puerto Rico
	AMNH 94713	Puerto Rico
	AMNH 94714	Puerto Rico
<i>Hapalops elongatus</i> Ameghino, 1894	FMNH P13122	Santa Cruz Fm., Santa Cruz, Argentina
	FMNH P13133	Santa Cruz Fm., Santa Cruz, Argentina
	FMNH P13145	Santa Cruz Fm., Santa Cruz, Argentina
<i>Megalonyx wheatleyi</i> (Cope, 1871)	AMNH 140854	Smith Pit, Levy Co., Florida
	AMNH 140855	Smith Pit, Levy Co., Florida
	AMNH 140855 A	Smith Pit, Levy Co., Florida
	AMNH 140855 C	Smith Pit, Levy Co., Florida
	AMNH 140855 D	Smith Pit, Levy Co., Florida
	AMNH 99186	Smith Pit, Levy Co., Florida
<i>Octodontotherium grandae</i> Ameghino, 1894	FMNH 13512	Santa Cruz Fm., Argentina
	FMNH P13507	Santa Cruz Fm., Argentina
	FMNH P13583	Santa Cruz Fm., Argentina
<i>Scelidotherium</i> sp.	FMNH P14450	Aravcano Fm., Corral Quemado, Argentina
<i>Thinobadistes segnis</i> (Hay, 1919)	AMNH FAM 102658	Mixson's Bone Bed, Levy Co., Florida
	AMNH FAM 102659	Mixson's Bone Bed, Levy Co., Florida
	AMNH FAM 102672	Mixson's Bone Bed, Levy Co., Florida
	AMNH FAM 102679	Mixson's Bone Bed, Levy Co., Florida
	AMNH FAM 102681	Mixson's Bone Bed, Levy Co., Florida
	AMNH FAM 102698	Mixson's Bone Bed, Levy Co., Florida